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Investigating a Competitive Two Species System that Produces Oscillations

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Abstract

The interactions between two species can have great influences on the ecosystem scale. A mathematical model, based on the model by Gilad *et al.* (2007) for water limited systems, represents a two species system with a tradeoff between the species. One species is an ecosystem engineer and is responsible for the increased infiltration. The other species is dependent on the first for its water but has, according to the tradeoff, a better resource uptake strategy. The tradeoff leads to oscillatory behavior under the right conditions. This oscillatory behavior can be interpreted as cyclic succession, the initial step of the “Biodiversity Cycling Hypothesis” (BCH) (Shachak *et al.* 2009). According to this hypothesis the ecosystem engineer is termed the Landscape Modulator Species (LMS) and the second species the Modulator Dependent Species (MDS). The model outcome is compared to fieldwork for the purpose of a field example and validation. The fieldwork compares the species *A. serratulooides* and *N. mucronata* to the LMS and MDS respectively, in accordance to modulation effect and resource uptake ability. The results are used to conclude the effects of cycling on hysteresis. These influences cannot be drawn from the results due to the occurrence of chaotic behavior. The extent of hysteresis is severely dependent on the initial conditions of the simulation.

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Introduction

Ecosystem Engineers

Ecosystem engineers are organisms that have the capability to change a given abiotic factor, changing the local environment and habitat with its presence (Jones *et al.* 1994). The change can be done by changing materials in the environment (allogenic ecosystem engineers) or by the organism changing itself (autogenic ecosystem engineers) (Jones *et al.* 1994). The term 'Ecosystem Engineer' has been used for 15 years and was first brought to the public by Jones *et al.* in 1994. There are many examples of ecosystem engineers, ranging from beavers building dams to zebra mussels causing algal blooms. In my case I consider the ecosystem engineer to be a plant species that through different mechanisms has a positive effect on the availability of a limiting resource. I focus on arid environments, so water is the limiting resource.

Mathematical models simulate ecosystem consequences of ecosystem engineers in both spatial and temporal dimensions (Cuddington & Hastings 2004). In many models a positive feedback is at the core of the engineering effect to promote the survivability of the ecosystem engineer in relation to the ecosystem's limiting resource. When considering bogs and swamps the limiting resource is nutrient availability and when considering arid environments, water is the limiting resource.

The positive feedback in the model can often cause the formation of spatial patterns at a large scale (Wright *et al.* 2004) (Dekkers *et al.* 2007) (Ridolfi *et al.* 2006) (Kefi *et al.* 2008), varying from tiger stripes to labyrinths. These patterns are also found in different natural habitats, verifying the foundations of the models suggesting pattern formation (Rietkerk & van de Koppel 2008). Three examples of natural habitats containing the indicated patterns that are being modeled are muscle beds (van de Koppel *et al.* 2008) (van de Koppel *et al.* 2005), bog & peat ecosystems (Eppinga *et al.* 2009) (Eppinga *et al.* 2009) and arid ecosystems (Borgogno *et al.* 2009) (Gilad *et al.* 2007) (Kefi *et al.* 2007) (van de Koppel *et al.* 2004) (Manor & Shnerb 2008) (Meron *et al.* 2007) (Meron *et al.* 2004) (Ridolfi *et al.* 2008) (Sheffer *et al.* 2007) (Sherratt 2005) (Xu *et al.* 2009) (Yizhaq *et al.* 2005). Several models exist explaining the formation of patterns in arid ecosystems, sometimes using different feedback mechanisms. An example of such a feedback mechanism in arid ecosystems is a root feedback. In this feedback the roots cause the soil around the plant to break up and become more porous allowing more water to infiltrate. Increased soil water content near the plant allows for more uptake and thus growth, assuming water is the limiting resource. Increased growth results in more roots and thus more infiltration. The model developed by Gilad *et al.* (2007) has implemented an elegant and extremely functional root feedback

mechanism. Therefore this investigation will be founded on their model and more details concerning the feedback mechanism will follow in the methods section.

The concept of ecosystem engineer can be put into an ecosystem development context as an ecosystem pioneer. The pioneer species colonizes bare land and modulates the local habitat through its ecosystem engineering ability. The increase in availability of the limiting resource caused by the pioneer allows different species, which were unable to colonize before the modulation, to enter the ecosystem. These colonizing species, which are dependent upon the pioneer to enter the ecosystem, will most probably be hostile to the pioneer because they compete for the same limiting resource. These new species may have their own effect on the local habitat again changing the range of species capable of growing. During ecosystem development new species colonize the modulated system and biodiversity increases. However if there are limited resources and catastrophic events occur regularly preventing development to a stable state, temporally cyclic behavior of the biodiversity appears. This cyclic behavior is termed “Biodiversity Cycling” (BC) by Shachak *et al.* (2008).

Biodiversity Cycling Hypothesis

A hypothesis concerning BC termed "Biodiversity Cycling Hypothesis" (BCH) sums up local biodiversity development and decay when considering biotically modulated landscapes. It is based on a combination of two different processes. The first is that the pioneer species modulate the habitat by forming patches. These species are termed “Landscape Modulators”. The second is the effect of modulation on species assemblages. The modulation causes a shift in the species capable of infiltrating into the habitat through a process called “Species Filtering”.

When considering landscape modulators two landscape properties control species filtering that of unmodulated and modulated landscape patches. Combining these two properties through the perspective of species filtering gives four functional groups of vegetation, grouped according to their local ecological niche. They are the; landscape modulator species, modulator-dependent species, unmodulated-dependent species, and independent species.

1. The landscape modulator species (LMS) alter local resource availability. They specialize on colonization rather than on resource competition. As a result their strategy is to colonize areas where other species cannot grow.
2. The modulator-dependent species (MDS) thrives in the area altered by the LMS. They are highly competitive for resources compared to the LMS as they have the same niche yet focus more on competition. They may coexist with the LMS or outcompete the landscape modulator, leading to a highly dynamical relationship.

3. The unmodulated-dependent species (UDS) thrive on un-modulated patches. They have no apparent modulation effect. There are high levels of competition between these species and the LMS for water. However after LMS establishment is the UDS are outcompeted due to their intolerance to the modulation.
4. The independent species (IS) are not influenced by the modulation. They can be seen as a group of species that exploit a separate niche with negligible competition.

Considering these four groups of species there will be a dynamical functionality in the ecosystem. The relations between the LMS and MDS in terms of their interactions are discussed, as they are important for the determination of their relationship.

Species Interactions

Competition and facilitation are the main interactions between the four groups. Some claim facilitation to be more dominant in arid environments (Bertness & Callaway, 1994) (Callaway *et al.* 2002) because the tolerance against limiting environmental condition is more dominant than competition amongst the individuals. Through the other perspective, competition may arise through exploitation of the same scarce resources (Tilman 1990), especially when using the same strategies.

In arid environments competition and facilitation are interactions through water availability. Plants can be seen as organisms that require the same resources to function; water, sunlight, carbon dioxide and nutrients. Therefore they are inherently competitive towards each other, especially when the resource is limited. However, how they obtain these resources may differ, leading to a decrease in competition. This is known as niche separation. Niche separation could account for the existence of the IS and is one of the theories of coexistence in general (Tilman 2004).

Many types of interactions between the LMS and MDS are possible. The interactions depend on how the species allocate resources to below and above ground biomass growth. This implies that vegetation has a limited amount of resources to allocate to different plant organs thus a tradeoff between allocation to below or above ground organs exists. Two species that are within the same niche yet differ in their investment for colonization (seeds or modulation capability) versus competition (taller stems or longer roots) represent a typical LMS/MDS interaction.

The interactions between the plant species *Ambrosia dumosa* and *Larrea tridentate* (McAuliffe, 1988). *Ambrosia dumosa* has the ability to grow where *L. tridentate* cannot as it has invested more in colonization. Therefore it can be considered to be a LMS that increases local water availability. Other species can take advantage of the ecosystem engineering ability

of the plant. Therefore the plant that has invested more in competition, *L. tridentate*, replaces *A. dumosa* in many cases and can be considered a MDS. Evidence for this view is that almost no young *A. dumosa* plants grow in the vicinity of an adult *L. tridentate* and that 85% of the young *L. tridentate* grow in the vicinity of adult *A. dumosa*. Often animals burrow near the root systems of *L. tridentate* causing it to die making the patch barren again, representing a perturbation specific to the MDS. *A. dumosa* can then colonize the barren patch in order to start the same cycle again. The fact that *L. tridentate* outcompetes *A. dumosa* and then dies due to its own shortcomings implies a short succession cycle.

The succession example above indicates the competition vs. colonization tradeoff (Tilman, 1990). This theory accounts for different dominant characteristics under different conditions, depending on their most limited resource (Tilman, 1990). Each species could allocate different portions of its limited energy to the organs responsible for satisfying exploitation of; soil resources, sunlight and germination site or developing resistance to herbivory. The species that allocates more energy to its germination site is a better colonizer. Species that allocate more energy to acquiring soil resources is the better competitor. Tilman (1990) introduced the idea of R^* , being the equilibrium soil resource level that is reached through consumption by a plant species. R^* is species-specific, the species with the lowest R^* will eventually outcompete the others. When two species have an equal R^* value they will coexist. If the resource concentration changes, a shift will arise in optimal energy allocation, closely resembling the shift in species filtering discussed earlier.

For my investigation I selected two species that I assumed to represent the initial stages of BC where LMS is replaced by MDS. The species are *Atractylis serratuloides* and *Noaea mucronata* which are two shrub species that grow in the Negev desert of Israel. *A. serratuloides* is assumed to be a colonizer and to accumulate soil under its canopy. Over time this accumulated soil forms a mound that grows as the canopy grows. It is believed that this mound has an accumulative characteristic concerning both water infiltration and seed deposition (Boeken & Orenstein, 2001) (Boeken & Shachak 1994) (Wright *et al.* 2006). Both would result in a positive feedback, as more water would allow the organism to grow more and more seeds would allow for more individuals to grow on the mound. *N. mucronata* does not have such engineering properties but grows in the same patches, often on the mounds constructed by *A. serratuloides*. This means that *N. mucronata* uses an alternative strategie to acquire water. A strategy is to become more competitive for water, but still being dependent on the engineering by *A. serratuloides* for germination. It can do this by extending its root system to absorb more infiltrated water, preventing other species from absorbing the water. Another strategy is to utilize a separate niche, although seeing as they are both woody shrubs

this is unlikely. If cycling could be established and the two species can be shown to have their own strategy for survival this could be an example of LMS and MDS relationship.

Clemens (1916) had an alternative way of looking at the succession cycle above. He proposed there are two main mechanisms by which succession can take place. One is through changes from outside the system, termed allogenic succession. An example is that a fire or a tree falling changes the conditions of the local habitat, enabling other species to establish. The alternative to allogenic succession is autogenic succession. In this case the change comes from within the system, for example a species modifies its habitat in such a way that it becomes more favorable for another species. This is a form of changes in species filtering.

In environments where soil resources are limited I suggest that the dominant tradeoff is between colonization ability and soil resource uptake. This tradeoff may describe how the LMS and MDS interact through the resources available. The LMS focus on colonization (dispersal methods and germination conditions) and the MDS focus on resource uptake (root biomass and resource use efficiency lowering its R^*).

Gurney & Lawton (1996) looked at the population dynamics of ecosystem engineers. They suggested that species that modulate their environment in order to survive could lead to either stable and deterministic equilibria, or they can lead to endogenous cycles. These cycles suggest a cyclic behavior between ecosystem engineers and species dependent upon their engineering. The interactions between the LMS and MDS can be compared to a predator-prey system. The LMS would be the prey as it supplies the MDS with sufficient water to grow, making MDS growth dependent on the LMS availability. The competitive ability of the MDS causes stress for the LMS. The stress results in a loss of biomass for the LMS, indirectly making the MDS the predator. This negative feedback of MDS on itself should result in a damping effect. Under the right conditions this can also result in oscillations of biomass levels for both species. These oscillations could be interpreted as biomass or succession cycles, giving us a basis for the cyclicity found in the BCH.

Problem definition, aim, and research question

With changing weather patterns increasing amounts of ecosystems are threatened by desertification (Borgogno *et al.* 2007) (Ridolfi *et al.* 2008). Therefore the economic value of these ecosystems through livestock agriculture is also at risk. Research in catastrophic shifts of single species systems (Rietkerk *et al.* 2004) (Borgogno *et al.* 2007) showed that overexploitation of such ecosystems can be permanently devastating, resulting in the loss of biodiversity. By investigating the stability of a two species system where one of the species is an engineer the idea of permanent devastation can be elaborated on.

Oscillations in two species vegetation systems in the context of ecosystem engineers in arid environments have not been thoroughly investigated. The addition of a MDS can either improve the stability of the system or it can decrease stability through causing temporal oscillations. The conditions that are necessary for the possible outcomes are unknown. Investigating these conditions can shed light over the possible outcomes and their implications on a larger scale.

This research looks at the mechanisms through which barren desert patches are colonized by ecosystem engineers and their consequences for biodiversity in dynamic ecosystems. The formation of desert ecosystems is important to know for the following reasons. First it shows the fundamental mechanism by which desert ecosystems work and portrays much of how organisms function by landscape modulation in resource deprived areas. Secondly it provides clues how we may combat desertification through re-colonizing and re-vegetating deserted areas by managing local landscape for biodiversity. A decrease in desertified areas will be beneficial to mankind through increased economic potential and increase in natural resilience to perturbations.

The aim of this research is to create a model that represents a two species system in an arid environment that can resemble the basics of the BCH, in the form of a short succession cycle. The model will provide a basis to investigate the characteristics of the two species that can make them resemble the LMS and MDS. By doing so it will also resemble an indirect predator-prey system. This can be achieved by finding parameter conditions that cause cyclicity of the biomass values. The analysis of bi- or multi- stability will allow finding hysteresis in the two species system. Ultimately the effect of oscillations, and the parameters influencing the oscillations, on hysteresis can be determined.

Fieldwork concerning *A. serratuloides* and *N. mucronata* provides an example of a cyclic two species system in an arid environment. The characteristics of the two species will indicate what parameter values are necessary to obtain oscillations from the model and properly represent the LMS and MDS. The oscillation depends on the engineering effect of the LMS and the competitive capability of the MDS. This can be found by measuring the root systems of the two species. More specifically finding the ratio between above ground biomass and lateral root length.

Determining the succession order of the example concerning *A. serratuloides* and *N. mucronata* is important for establishing basic understanding concerning BC in the area. The order of succession can be studied by observing: 1) the soil mounds at the base of the plant. 2) The plant species and 3) The age of the plant (represented by its size) The order of succession

also entails the effect on species filtration, as the mound is responsible for increased water infiltration.

Research questions & hypotheses

1. What are the possible outcomes of the mathematical two species model representing the LMS and the MDS and under what conditions do they appear?
 - H1. A two species system per definition has four different possible outcomes. These four outcomes are the different equilibrium positions of biomass levels over time, being the zero state (0,0) the two pure states (LMS,0) and (0,MDS) and the mixed state (LMS,MDS). Next to these four equilibrium states an oscillation state is possible in which either one or both biomass levels do not reach equilibrium and remain oscillating over time. This is a complicated form of the pure and mixed states and will occur for a precipitation range similar to that of a desert.
2. Are there signs of hysteresis in the system? How do oscillations influence hysteresis?
 - H2. Oscillations, at the ecosystem level, are a mix of all the different equilibrium states. When testing for hysteresis by changing the bifurcation parameter the state of the system could be any of the four equilibrium states when the bifurcation point is reached. This will lead to different initial conditions at the bifurcations point for different simulation lengths. Different initial conditions at the bifurcation point should lead to chaotic behavior.
3. Can the interactions between *A. serratulooides* and *N. mucronata* represent a short succession cycle?
 - H3. Because of its canopy architecture *A. serratulooides* functions as the ecosystem engineer forming mounds and raising soil moisture. Therefore its canopy size, as a covariate of age, is strongly correlated to the size of the mound. *N. mucronata* is the nurse plant protégée, it germinates on established mounds.
 - H4. The size of the mound dictates the amount of water infiltration and thus also the eventual size of the plant occupying it. This means that an old individual will be closely correlated to its corresponding mound with respect to size, whereas the size of young individuals may not correlate with the size of the mound.
 - H5. The root size of *A. serratulooides* is small, relative to the mound (and above ground biomass), while the root system of *N. mucronata* is wider than that of *A. serratulooides*. The ratio between above ground biomass and lateral root length is lower for *A. serratulooides* than for *N. mucronata*.

- H6. Perturbations such as grazing affect *N. mucronata* more than *A. serratuloides*. Grazing decreases the relative amount of above ground biomass compared to the other variables measured, though more for *N. mucronata* than for *A. serratuloides*.
4. Are the parameters that represent LMS and MDS in the model representative of the parameters found in the field for the *A. serratuloides* and *N. mucronata* two species system?
- H7. The parameters found in the field should resemble the parameters found in the model.

Methods - Model

The Lotka-Volterra model is the simplest form of a modeling predator-prey system. In this model the growth term of the prey is dependent only on the amount of prey, whereas the death term is dependent on both the number of prey and the number of predators. The predator growth term is dependent on the amount of predators and the amount of prey and its death term is dependent only on the amount of predators. The mixed state stability point of this model is an imaginary Eigen value after linear stability analysis and so the model conforms to a constant motion. This means that the amount of both predator and prey will remain oscillating over time. From this it can be derived that in order to get oscillations in a two species system the growth and death rates of the predator and prey should resemble the same inter-dependencies as in the Lotka-Volterra model.

Fussmann *et al.* (2000) investigated a live predator-prey system and, for comparison, constructed a model with three state variables; nutrient density, algae density and planktonic density. Their goal was to investigate a multi-species system that could be modeled and show population cycles. They achieved this by varying the nutrient availability in the experiment. Their population cycles exhibited the oscillatory dynamics predicted by mathematical models. Similar models have led to the proposition that fluctuations in populations may have a natural internal mechanism (May, 1972).

A dynamical mathematical model will be made to represent the desert ecosystem. The model will be based on the models constructed by Gilad *et al.* (2007), but it will not be spatially extended. One of the models focuses on the root augmentation feedback and the other on investigating the interactions between multiple species. Both are necessary for this investigation.

It will consider soil water as a limiting resource together with the biomass of the two species as the dependent variables. One species will have an influence on the infiltration of the system to represent the colonization ability of the LMS. The infiltration of bare soil is held at

a low value to emphasize the influence on infiltration of the LMS. The other species will have a larger root system, meaning it can take up more water and compete better than the first species, making it the MDS.

Formulas

dB_{LMS}/dt is the variable that represent the change in above ground biomass over time for the LMS ($kg\ yr^{-1}$). dB_{MDS}/dt is the variable that represent the change in above ground biomass over time for the MDS ($kg\ yr^{-1}$). Refer to Table 1 for units.

$$\frac{dB_{LMS}}{dt} = G_{LMS}B_{LMS}(1 - B_{LMS}/K_{LMS}) - M_{LMS}B_{LMS}$$

$$\frac{dB_{MDS}}{dt} = G_{MDS}B_{MDS}(1 - B_{MDS}/K_{MDS}) - M_{MDS}B_{MDS}$$

G represents the biomass growth rate and represents a plants ability to compete for resources. The term $(1-B/K)$ is used in population equations in order to limit the maximum allowed biomass. The carrying capacity K determines the maximum tolerated level of biomass that the ecosystem can contain in the case that water is no longer limiting, because dry ecosystems have other limiting factors such as parasites. M is the rate of biomass loss due to mortality and all other effects (like grazing).

The growth rate term G is represented below.

$$G_{LMS} = \Lambda_{LMS} \cdot (1 + E_{LMS}B_{LMS})^2 \cdot W$$

$$G_{MDS} = \Lambda_{MDS} \cdot (1 + E_{MDS}B_{MDS})^2 \cdot W$$

Λ represents the plants growth rate per unit of soil water. E quantifies the root augmentation per unit biomass. The larger E is the stronger the feedback mechanism will be. These growth terms are non-spatial forms of Gaussian kernel taken from the original model. The original forms are spatially extended and thus need a square term. They are left in this form for the future possibility to return to the spatial form without having to change the formulas.

dW/dt is the variable that represents the change in soil water density over time ($kg\ yr^{-1}$).

$$\frac{dW}{dt} = I \cdot P - N(1 - R(\frac{B_{LMS}}{K_{LMS}} + \frac{B_{MDS}}{K_{MDS}}))W - (U_{LMS} + U_{MDS})W$$

I represents infiltration and will later be discussed in detail. P represents the precipitation and becomes a rate when combined with I. N is the soil water evaporation rate for bare soil. R is the reduction in soil-water evaporation rate due to shading and is dependent on the biomass of the two species.

I, the infiltration term is represented below.

$$I = A \frac{\Psi_{LMS} B_{LMS} + Qf}{\Psi_{LMS} B_{LMS} + Q}$$

A represents the infiltration rate in fully vegetated soil. Ψ is the relative influence per species on infiltration and as the LMS has all the influence for simplicity we made it 1 for LMS and 0 for the MDS, meaning we could

leave it out. Q is the reference biomass beyond which the plant approaches its full capacity to increase the infiltration rate. The parameter f , $0 \leq f \leq 1$, measures the strength of the positive feedback. For $f = 0$ there is a strong influence on infiltration and a value of 1 being no influence of biomass on the infiltration rate. The LMS is the only species that has an effect on the infiltration. If $B_{LMS} = 0$ then the infiltration term equals $A \cdot f$. If $B_{LMS} = K_{LMS}$ then the infiltration term approaches A. This is part of the infiltration feedback mechanism. The overall influence is represented in figure 1.

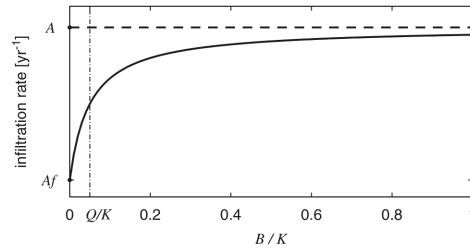


Figure 1. The influence of biomass on the infiltration rate. As the biomass reaches its critical value K the influence on infiltration saturates towards A. (Taken from Gilad *et al.* 2007)

The soil water consumption rate, U is shown below.

$$U_{LMS} = \Gamma_{LMS} \cdot (1 + E_{LMS} B_{LMS})^2 \cdot B_{LMS}$$

$$U_{MDS} = \Gamma_{MDS} \cdot (1 + E_{MDS} B_{MDS})^2 \cdot B_{MDS}$$

Γ is the soil water consumption rate per unit biomass. These are the same for both species. As was done in the growth term the Gaussian kernel was derived from the spatial form, resulting in a square term.

There are three differences between the LMS and the MDS. The first is that only the LMS has an influence on infiltration, making it the only ecosystem engineer. The second difference is that the MDS has a larger root augmentation per unit biomass (E). This allows it to be more competitive in the presence of water. The last difference is that the MDS has larger mortality, M. The last condition is not necessary for oscillations to occur but allows them to occur at more realistic values.

Table 1 Units and Description of the Used Parameters. The values are taken to be the same as or near to the values used in Gilad *et al.* (2007).

Parameter	Units	Description	Value/range
K	kg	Maximum standing biomass	1
M	yr ⁻¹	Rate of biomass loss due to mortality and disturbances	0-10
Λ	kg ⁻¹ yr ⁻¹	Biomass growth rate per unit soil	0.032
E	kg ⁻¹	Root's augmentation per unit biomass	0-20
P	kg yr ⁻¹	Precipitation rate	0-1000
N	yr ⁻¹	Soil water evaporation rate	4
R	-	Evaporation reduction due to shading	0.95
A	yr ⁻¹	Infiltration rate in fully vegetated soil	40
Ψ	-	Relative influence on infiltration of the species	1
Q	kg	Biomass reference value beyond which infiltration approaches maximum	0.05
f	-	Infiltration contrast between bare soil and vegetated soil	0.01
Γ	kg ⁻¹ yr ⁻¹	Soil water consumption rate per unit biomass	20

Equilibrium state definition

For two species four different equilibrium states can occur. The annotation for the states will conform to the (LMS,MDS) convention. The first state is the bare state, annotated by (0,0), and implies that both species are absent (or present in very small numbers). The second state is the pure LMS state, annotated by (LMS,0). The third state is the pure MDS state, annotated by (0,MDS). The last state is the coexistence state, annotated by (LMS,MDS).

For visualization purposes after the simulation the presence of a species is determined by comparing the actual biomass level to the maximum biomass value, K. When the actual is between 5% and 100% of K it is said to be present. Next to these four states there is also an oscillatory state. In order to determine whether the ecosystem is oscillating the maximum and minimum biomass values of the last half of the simulation are compared for both species. If they are found to be different by more than 10% or more of K value the ecosystem is oscillating. Note: this may result in random locations being indicated as oscillating as the difference within the second half of the simulation is larger than 10% of K without actual oscillations taking place. Even though the definition is not perfect it will suffice for the task at hand.

ODE solver and Average Biomass values

Different ODE solvers provided by Matlab were used. Sometime a faster solver was needed because the same simulation needs to be run 10.000 times for one plot, whereas other simulations could use more time consuming and exact solvers. Due to the changing nature of the solver a universal method needed to be developed to calculate the average biomass value for the whole simulation. This universal method was achieved by integrating the time-

biomass plot to get the total area under the curve and then dividing this by the time of the simulation.

Simulation Plans

The main difference between the LMS and the MDS is found in the infiltration ability, the water uptake ability (through the root augmentation) and mortality. The values for the LMS are kept constant to resemble the ecosystem engineer of Gilad *et al.* (2007).

When entering all the parameter values simulation can be run to create a time profile. These plots are generally run for 100 years, long enough for the system to reach equilibrium. These plots show the value of the three different state variables over time.

A parameter plot allows finding a valid parameter range of the MDS for the root augmentation (E_{MDS}) and mortality (M_{MDS}). This parameter plot indicates which of the four possible equilibrium states the two species system will evolve to over time. Next to the equilibrium states there is also a state in which no equilibrium is reached. In this case the system remains dynamic and oscillates over time. This state is also represented in the plot. The plots will be divided into different areas according to the dominant equilibrium state. These parameter plots are made four times, one for each possibility of initial conditions (being (0,0), (LMS,0), (0,MDS) and (LMS,MDS)). This gives a clear idea of the influence of the initial condition on the outcomes of the simulations for the different parameter values.

Parameter plots for the average biomass values for both LMS and MDS for the same values of M_{MDS} and E_{MDS} will also be calculated, showing the effect of a change in a parameter value on the plant presence.

In order to determine the importance of precipitation on the dynamics of the model precipitation is also varied. However it is not the only possible environmental factor. Mortality can be considered both a species (or internal factor) characteristic and an environmental (external) factor due to its general nature and definition. An example of the influence of the external factor on mortality is grazing. An example of an internal factor is resistance to grazing, by for example growing of thorns. This costs energy that can no longer be invested in other organs but results in less grazing and so in this form is a tradeoff. A parameter plot shows the equilibrium states of these two parameters, M2 and P, using a value for E2 determined by the previous parameter plots. These plots will indicate where bi- or multi- stability can be found.

In addition to the average biomass plots, productivity plots are made. These plots show the productivity of the system by simply adding the average biomass values of the two species. From these plots the productivity of the equilibriums state can be deduced.

Methods - Fieldwork

Background

In addition to the model that is being constructed it is beneficial to do fieldwork in order to portray an example of what the model is simulating. In order to connect the model to reality it should be verified in the field. The main theory behind the model considers the idea of 'biodiversity cycling' (Shachak *et al.* 2008) and the terms 'Landscape Modulator Species' (LMS) and 'Modulator Dependent Species' (MDS). The following examples are hypothesized and conform to the terminology utilized by Shachak *et al.* (2008).

The LMS, in our case *Atractylis serratuloides*, acts as the ecosystem engineer raising soil moisture content. It modulates the landscape by building up a soil mound that increases infiltration under its tight canopy. I assume that this shrub has a small lateral root system.

I assume that *Noaea mucronata*, does not thrive on an exposed surface as the LMS does. For establishment it requires increased soil water levels that can be found around the LMS and it is therefore dependent on the LMS. I propose that after it is established, its laterally larger root system allows it to tap into a larger soil volume. If this includes the rooting space of the LMS, the MDS may compete with the LMS, with or without light interference by the canopy of the MDS. This can result in suppression and death of the LMS. Eventually, the dependence of the MDS on the LMS for soil water can lead to its own demise when the conditions are right, giving rise to a cycling characteristic.

Study Area

The plant samples (root and canopy) and the soil mound samples to test the above ideas were taken from an area of arid shrubland at Shaked Park near Ofakim, Israel. The area was fenced to exclude the effect of grazing, although grazed samples were taken outside the fence. The mean annual precipitation is about 200 mm per year, although it is highly irregular and variable. The precipitation is limited to the winter season (October-April). There is not a wide variety of shrub species at the site. The shrubs have peak biomass values around April, at the end of the rainy season (Wilby & Shachak, 2000). In addition to shrubs there is high species richness of annuals and geophytes (Boeken & Shachak, 1994). Between the patches of shrubs there is a well developed biogenic soil crust formed by cyanobacteria, algae, mosses and lichens (Zaaky & Shachak, 1994).

Data Collection

The data on the two species in relation to their above ground biomass and root system was collected, during the dry season in June 2009. The data was collected after two years of drought. For both species 13 individuals of different sizes were selected for monitoring

above ground biomass and the length of the root system. In addition, a general survey of about 30 individuals per species was conducted both within and outside the fencing. In the survey canopy diameter and mound diameter were measured. The protocol of the fieldwork is described in Box 1 is followed.

Box 1. Protocol

- 1 Take a photograph from above with the reference ruler and measure the diameter in two directions of the biomass patch.
- 2 Remove the above ground biomass and place in a numbered bag.
- 3 Take a photograph from above with reference ruler and measure the diameter in two directions of the mound.
- 4 Remove the mound and place it in a numbered bag.
- 5 Dig a cross section of the root system and follow roots as far as possible. Measure the lateral length of the dug out roots.
- 6 Take a photograph of the root system.
- 7 The weights of the samples are measured in the laboratory.

Statistical Analyses

The successional order is visualized by plotting the results of the survey (Canopy radius Vs. mound radius). Pearson's correlations indicate the relations between canopy radius and mound radius for the two species and their significances. The differences between the Pearson's coefficients of the two species indicate the difference in successional order. The difference is due to a closer relation between a canopy and mound for a species that causes mound formation by the canopy. A species that is dependent on an already formed mound to grow will be found more frequently on a mound larger than itself as it arrived later than the mound is constructed. Therefore this plot intrinsically also indicates the infiltration effect, Ψ .

Plotting lateral root length against above ground biomass indicates the root augmentation values for the two species. Pearson's correlation indicates the relation and its significance. The different correlation coefficients represent the different E values. The root augmentations value is needed to compare the water uptake ability of the two species. If one species has larger water uptake ability than the other it will be more competitive in an arid environment.

The influence of grazing is indicated by plotting canopy radius against mound radius for both the grazed and ungrazed condition for both species. Pearson's correlation indicates the relation between mound radius and canopy radius for the two grazing conditions and the two plants. It is also responsible for the determination of significance for all the relations.

Results - Model

Parameter Space

Four plots in parameter space for two parameters, both determining the characteristics of MDS species are presented (Fig. 2). M_2 , on the y-axis, is the mortality coefficient (its function is described in the methods) determining the percentage of total biomass of that species to subside per time unit. E_2 , on the x-axis, is the root augmentation (its function is also described in the methods section). As both parameters determine characteristics of MDS the plane describes an outcome of the two species system determined by MDS. This allows one to determine the characteristics of the species according to the outcome of the whole system.

The difference between the a,b,c & d figures is the initial conditions. Figure 2a has initial conditions (0,0) and represents an initially empty ecosystem that can be colonized by this two species system. Figure 2b has the initial condition (LMS,0) that represents an ecosystem where LMS is dominant and MDS is not present but does have the ability to colonize if the conditions are favorable. Figure 2c has initial conditions (0,MDS) that represent an ecosystem dominated by MDS but now the LMS has the ability to colonize if the conditions are favorable. Figure 2d has initial conditions (LMS,MDS) that represent a coexistent ecosystem.

In all four figures there are three main areas represented by the colors **turquoise**, **green** and **yellow** (Fig. 2). These colors represent different equilibrium states. Next to these three main areas is an area of colored bands that also contain **blue** and **red**.

The first state is the domination of LMS referred to as the (LMS,0) state. It is represented by the **turquoise** color and is found, in general, in the top left corner. This represents high mortality and low root uptake ability of the MDS. Because of these two less competitive characteristics the LMS species dominates.

The second state is the domination of MDS referred to as the (0,MDS) state. It is represented by the **green** color and is found, in general, in the bottom right corner. This represents low mortality and high root uptake ability of the MDS. Because of these two more competitive characteristics the MDS dominates. Within this area there are bands showing two new colors, **blue** and **red**. Blue represents the (0,0) state and red the oscillatory state. These two will be elaborated on later. There is also a band of turquoise again that will also be elaborated on later.

The third state is the coexistence of both species and is referred to as the (LMS,MDS) state. It is represented by the **yellow** color and is found, in general to extend from the bottom left

corner to the top right along the division line between the (LMS,0) and (0,MDS) state, the extent depending on the initial condition. The bottom left and along this division line, where there is coexistence, represents an area where the advantages of one characteristic of MDS are outweighed by the disadvantages of the other characteristic. This results in general characteristics where both species are so similar and equally competitive that it results in their coexistence.

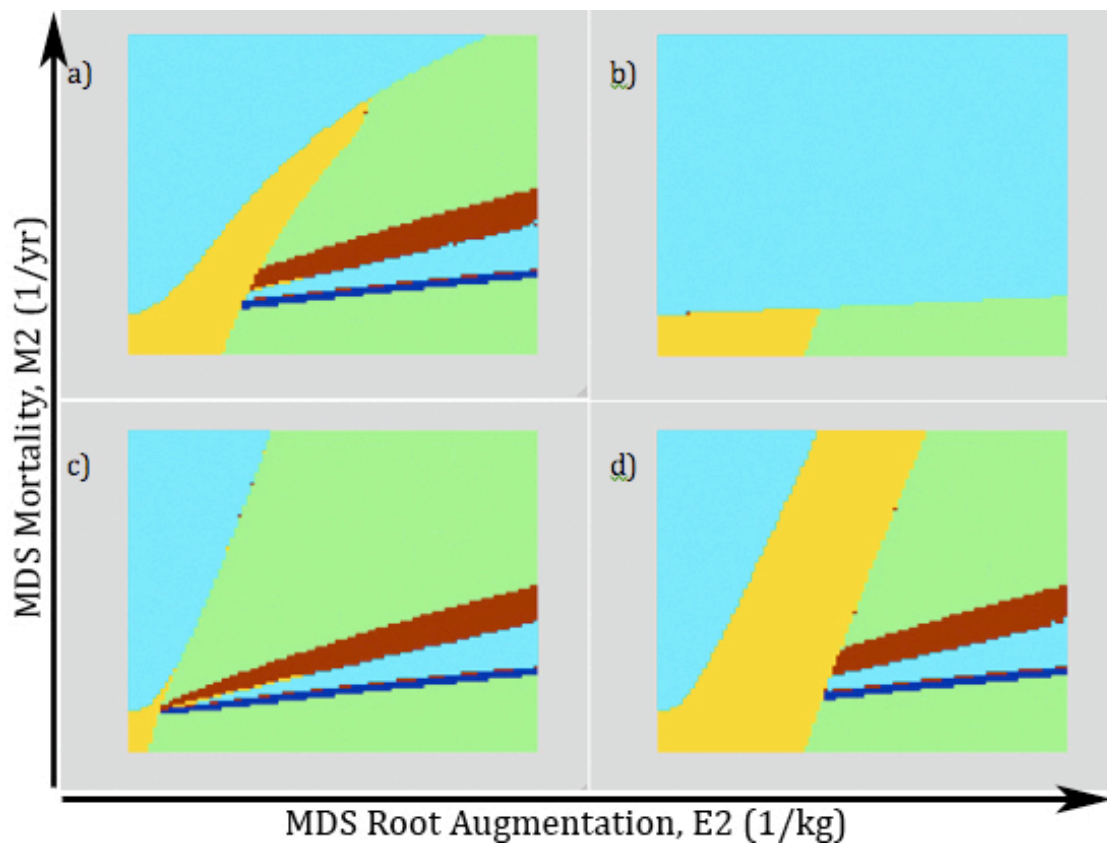
Between the four figures there are some interesting differences. The more neutral and unbiased initial conditions of figure 2a (0,0) and 2d (LMS,MDS) show a large area of coexistence (yellow). The boundary between the (LMS,0) state and the (0,MDS) state is in a different location for all four figures. The bands leading to oscillations are not found in figure 2b and their location in the other figures (2a, 2c & 2d) is the same. Figure 2c almost shows an origin where the bands of different colors come together.

Bands enclosed by the (0,MDS) state

The area of the (0,MDS) state is especially important as it contains bands of irregular states within itself. This area is comprised out of several different bands representing different states.

The (0,0) state band, represented by the **blue** color, is an equilibrium state where competition is so fierce that neither of the two species survives. This phenomenon will be termed ‘cross annihilation’ and can be thought of as ecological conditions where (co)existence is simply impossible due to harsh competition. During the time simulation both biomass levels rapidly peak and die out again after which the MDS always retains slightly higher numbers. This differs from the (0,0) state found at very low precipitation values, where there is no peak at all. This means there is a different dominant mechanism at work leading to this (0,0) state. This phenomenon does not occur where the LMS is dominant (Fig 2b). This is because MDS is suppressed under the M2 and E2 conditions necessary to achieve cross annihilation. The suppression results in no initial growth of the MDS and thus no interactions between the two species.

During the simulation of the (0,0) state, as both biomass values decrease towards zero the MDS numbers always remain slightly higher than those of the LMS. This creates a form of suppression of the MDS on the LMS. As long as this suppression is present the LMS will not grow and neither will its modulation effect. On the other hand if the MDS mortality is raised slowly it should eventually lift this suppression and result in the LMS dominating again. This is what happens in the next band, where the M2 is slightly higher.



Color	Eq. state (B1,B2)
Blue	(0,0)
Turquoise	(LMS,0)
Green	(0,MDS)
Yellow	(LMS,MDS)
Red	Oscillations (LMS,MDS) & (0,MDS)

Figure 2 Parameter Space Plots showing Equilibrium States. The above graphs can be split into three realms. Turquoise at the top left, green at the bottom right and in between yellow. The parameter values were chosen to be equal to or in the order of the values taken by Gilad et al. (2007). The legend with colors indicates the equilibrium state. Oscillation can be found in figures a, c & d. Figures a & c show largest realms of coexistence. **a)** Initial condition $(B1,B2) = (0.01,0.01)$. **b)** Initial condition $(B1,B2) = (1,0.01)$. **c)** Initial condition $(B1,B2) = (0.01,1)$. Figure c shows that oscillations may occur for the parameter ranges of $E2 > 2.3$ and $M2 > 2.2$. **d)** Initial condition $(B1,B2) = (LMS,MDS)$. **Conditions:** $0 < E2 < 20$; $0 < M2 < 10$; $E1 = 3.5$; $M1 = 1.8$; $P = 400$;

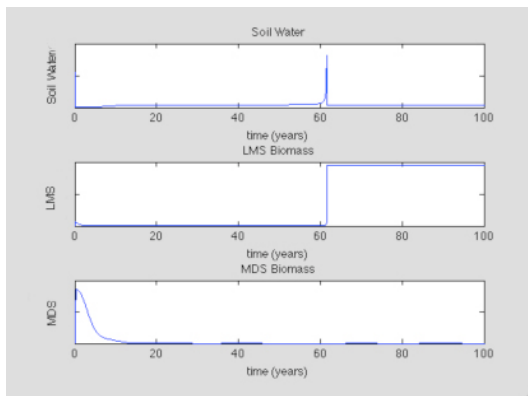


Figure 3 Time profile for soil water, LMS and MDS biomass for oscillating state band within the MDS dominance realm. ($E2=10$, $M2=2.6$)

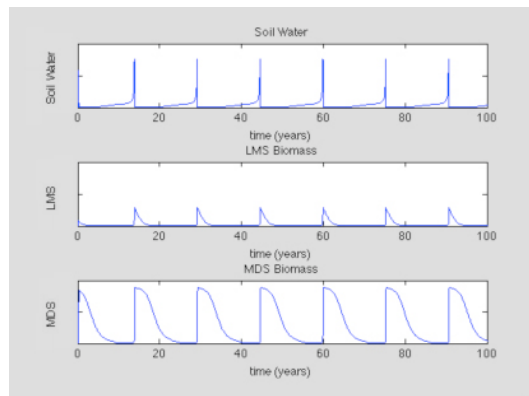


Figure 4 Time profile for soil water, LMS and MDS biomass for (LMS,0) state band within the MDS dominance realm. ($E2=10$, $M2=2.0$)

The next band (**turquoise**) is again a (LMS,0) state. Figure 3 shows its time profile. It shows that after 60 years there is a spike in soil water and rapid growth of LMS as result. This is implied by the gradual increase in soil water before the spike. The time period of 60 years does not apply to every point in the band and thus may vary. The MDS does not grow as a result of the spike in soil water. This would usually indicate a fault in the solver however all ODE solvers give the same result. This implies it is an intricate result of the model. More information regarding this spike phenomenon will follow when the average biomass values are plot.

Figure 4 shows a time profile for the **red** band. In this band the biomass levels periodically vary. It shows how in the beginning the biomass of the LMS species increases and allows for more water to enter the system. This allows MDS to consume most of the water with its larger root system and grow considerably. This growth leads to a depletion of the water and an annihilation of both species, terminating the modulation effect of the LMS species. This would result in cross annihilation. The reason no species would grow is that the MDS keeps suppressing the LMS even at tiny biomass values so the MDS prevents the LMS/ from growing again.

As the M2 value is further increased it results in the MDS diminishing faster than the LMS. This relieves the LMS from the suppression of the MDS, allowing the LMS to grow again, reinitiating the growth phase of both species. This in turn leads to its annihilation again. This cyclic character is found for slightly higher M2 values and will be referred to as oscillations, or the osc (LMS,MDS) state, and when both species are oscillating, is represented by a **red** color.

As M2 is further increased the biomass values for the LMS species gradually decrease until they are negligible. This gives rise to an oscillation state of solely the MDS yet is qualitatively the same as earlier behavior. It is referred to by the osc (0,MDS) state and for simplicity also has a **red** color. This implies that there should be conditions for an one species model where there are also oscillations. It should be emphasized that this oscillation state is found within the MDS dominance realm, implying that the LMS is interfering with the stability of the MDS.

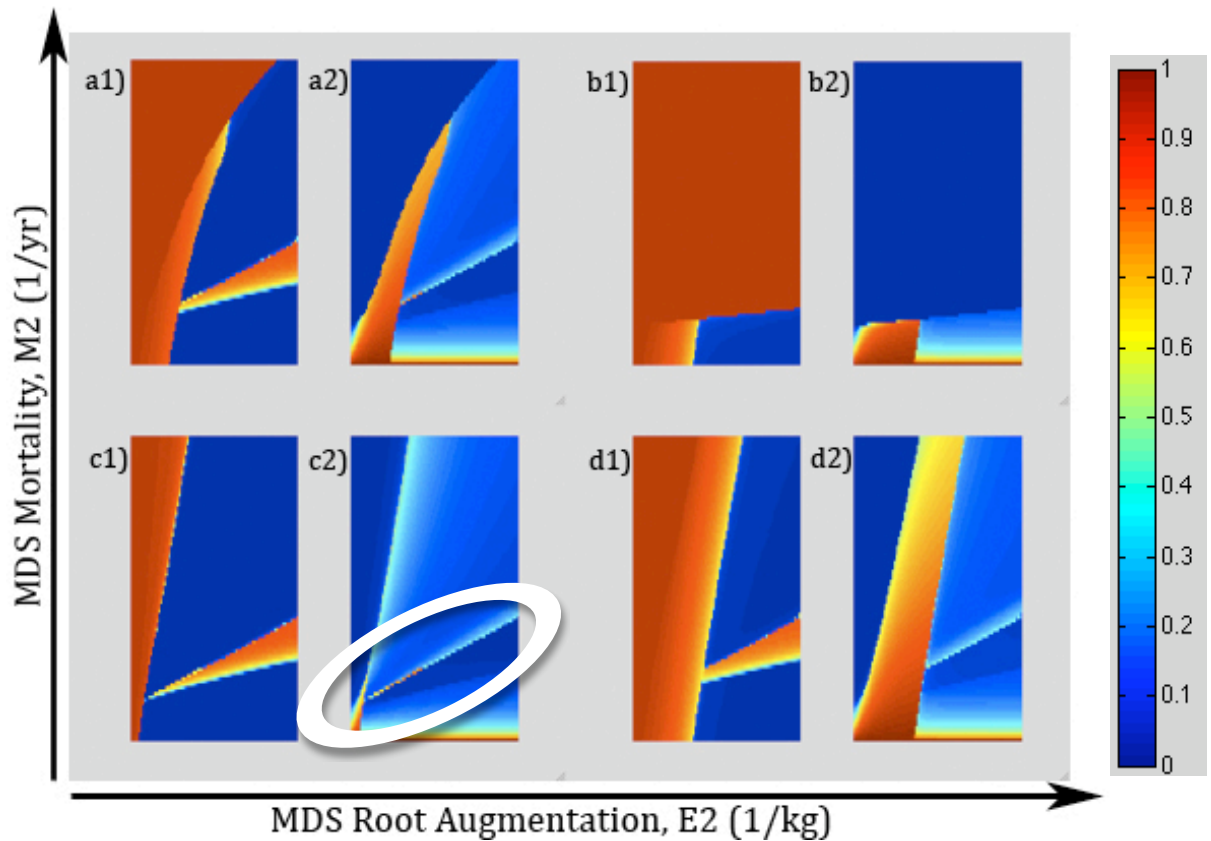


Figure 5 Parameter Space Plots showing Average Biomass Values for LMS (1) and MDS (2). When combined these figures can show what equilibrium state is found at any given location in parameter space, which is done to give figure 2. However it can give additional information, showing the exact average value of biomass for the both species. The letter indicates the initial condition used to achieve equilibrium and the number indicates the species. Figure 2 is derived from these figures and so the figures per initial condition are similar to those of figure 2 in form. The main difference now is that it is possible to focus on the level of average biomass, which is information left out of figure 2 for simplification. This information is given on a color scale, blue being the lowest level and red the highest. Right of the figures is a colorbar showing the biomass values per color. **a)** Initial condition $(B_1, B_2) = (0.01, 0.01)$. **b)** Initial condition $(B_1, B_2) = (1, 0.01)$. **c)** Initial condition $(B_1, B_2) = (0.01, 1)$. **d)** Initial condition $(B_1, B_2) = (LMS, MDS)$. **Conditions:** $0 < E_2 < 20$; $0 < M_2 < 10$; $E_1 = 3.5$; $P = 400$. The **circle** indicates the boundary between the osc (LMS, MDS) and (0, MDS) states. This area shows that oscillations occur for high LMS and low MDS biomass values.

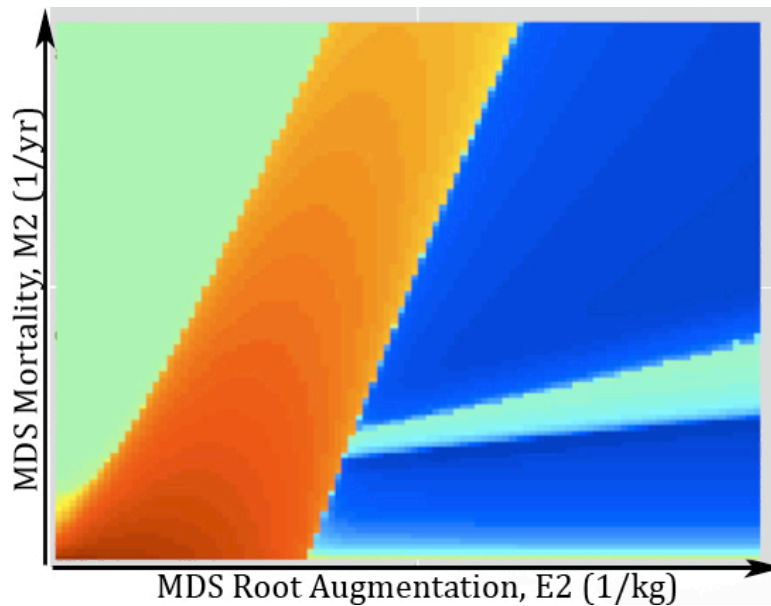


Figure 6 Productivity of the ecosystem. This figure shows the sum of the two values for the average biomass of the (LMS,MDS) equilibrium state shown in figure 5d. This sum can be considered to be the productivity of the ecosystem. It shows that the productivity is highest when there is coexistence and that the bands of instability result in higher productivity compared to the pure MDS state which is dark blue. The band within the MDS dominance realm shows higher productivity for the oscillating state than for the pure MDS state.

Average Biomass Values and Ecosystem Productivity

The most interesting information found in figure 5 that cannot be found in figure 2 is the top boundary between the area of the oscillation state and the MDS equilibrium state. These are found in figure 5a, 5c & 5d just above the bands of high LMS and low MDS within the MDS dominance range. If we look at the MDS plots we see the MDS levels slowly decrease from the bottom upward, going from brighter colors to dark blue, for the MDS equilibrium state. Eventually a dark blue band of MDS is found where the LMS prospers. This band, continuing upward, gives way to a brighter band of MDS where LMS goes back to dark blue. This is the boundary between oscillations (the bottom side of the boundary) and the new MDS equilibrium state but with heightened levels. It shows that the oscillations occur where average MDS biomass is low and average LMS biomass is high.

Adding the average biomass values for the two species together allows for a characteristic that is more general, concerning the whole system rather than the two species separately. This summation is the total amount of biomass in the system and can be considered the productivity of the ecosystem. The more biomass that is present the more productive, diverse and resilient a system generally is. However diversity cannot be measured in this case as it strictly considers a two-species system. Figure 6 shows great similarity to figure 5d and it clearly shows that the bands in the MDS dominance realm give heightened productivity of the

system. (Logical as generally LMS can have higher productivity because it consumes less water per unit biomass.)

Precipitation and Hysteresis

As can be seen most clearly in figure 7b the parameter space in figures 7a to 7d can best be divided into 4 different areas. On the left, with near to zero precipitation values, neither species survive leading to a (0,0) equilibrium state represented by a **blue** color. Then as precipitation is increased for high M2 values the LMS becomes dominant leading to a (LMS,0) state represented by a **turquoise** color. On the bottom left side as there is increasing precipitation the MDS dominates leading to a (0,MDS) state represented by a **green** color. From this state coexistence can be reached by increasing the precipitation or increasing M2. Figure 6a and 6d, the more neutral initial conditions again give rise to the largest coexistence areas represented by a **yellow** color. It is also evident that coexistence occurs in the MDS dominance realm. Figure 6c shows most clearly that by increasing precipitation under the right M2 values can give rise to a band of oscillations shown in **red** after passing through a band of LMD dominance. For decreasing precipitation the red band can be reached either through the green (MDS dominance) or yellow (coexistence) area.

From the origin of all four of the figures of figure 7 the MDS dominance realm follows a diagonal trajectory. From the figure it is not clear whether the MDS is present at the origin, where precipitation is zero. However when considering the formulas it is impossible for any species to exist without precipitation. If there is no influx of resources into the system there will also be no growth, and thus outflux. However at the origin the MDS mortality term is also zero so there is no outflux nor influx so the MDS remains at its initial condition, which is (0.01). According to the definitions used this means the origin is not a (0,MDS) dominance realm but MDS is present. This zero MDS mortality also explains why the whole bottom axis of all the figures is dominated by MDS. Once the precipitation is high enough to allow for coexistence at the bottom axis then LMS also prevails creating a coexistence (yellow) realm.

The equilibrium state plots show multi-stability. Multi-stability can be detected by taking one location in the space and comparing the dominant equilibrium state between the four graphs. For example, if we take the precipitation and MDS mortality value to be half the maximum for almost every plot the equilibrium state is different, (refer to x in fig. 7). In a) the x is in the green area, in b) it is in the turquoise, in c) it is green again and in d) it is in the yellow area. This means that for these parameter conditions the system can develop into multiple stable states depending on the initial conditions.

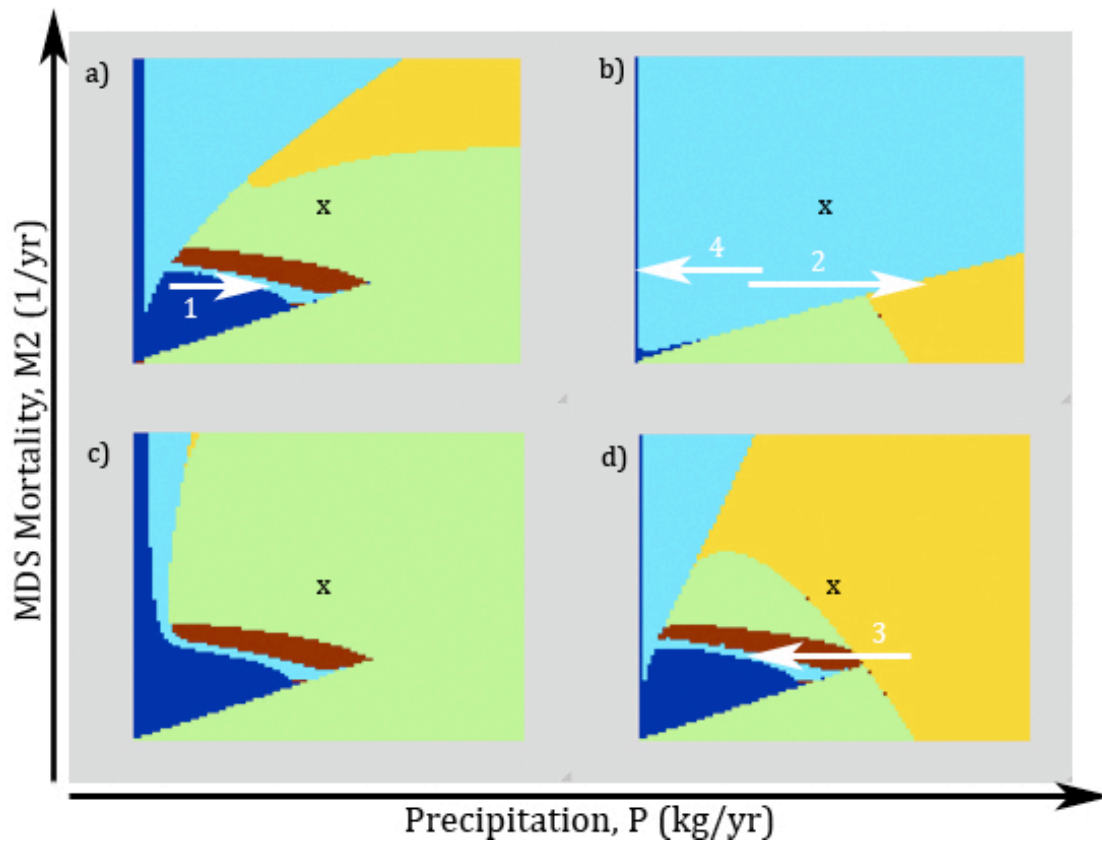


Figure 7 Parameter Space plots showing Equilibrium States for Precipitation and Mortality of MDS. Plots a to d show the same different initial conditions as figure 2 and 5 and the colors are the same as in figure 2. The above plots can be split into four realms. The **dark blue** is at the far left, **turquoise** at the top left, **green** at the center bottom and **yellow** at the right. **a)** Initial condition $(B1, B2) = (0.01, 0.01)$. **b)** Initial condition $(B1, B2) = (1, 0.01)$. **c)** Initial condition $(B1, B2) = (0.01, 1)$. **d)** Initial condition $(B1, B2) = (LMS, MDS)$. **Conditions:** $0 < P < 1000$; $0 < M2 < 10$ $E1 = 3.5$; $E2 = 10$; The **x**'s represent a location with the same values but different initial conditions resulting in different equilibria. The arrows represent hysteresis, where an arrow to the right is increasing precipitation and an arrow to the left is decreasing precipitation. Hysteresis can be seen when following arrow 1 from the dark blue $(0, 0)$ state to turquoise $(LMS, 0)$ state. Seeing as $(1, 0)$ are the initial condition for the turquoise state you must go to figure b, where you follow arrow 2 that ends in the yellow (LMS, MDS) state. For the (LMS, MDS) state the initial conditions are $(1, 1)$ so you must look at figure d. Now when decreasing precipitation you follow arrow 3 to the left and you enter the red (LMS, MDS) oscillating state. This state is a complicated form of (LMS, MDS) but for most of the time contains both species meaning you still look at figure d. When further decreasing you enter the turquoise $(LMS, 0)$ state and have to return to figure b again. The precipitation values for the return to the turquoise $(LMS, 0)$ state are different from the values for leaving the turquoise $(LMS, 0)$ state thus hysteresis is observed.

Color	Eq. state $(B1, B2)$
Blue	$(0, 0)$
Turquoise	$(LMS, 0)$
Green	$(0, MDS)$
Yellow	(LMS, MDS)
Red	Oscillations (LMS, MDS) & $(0, MDS)$

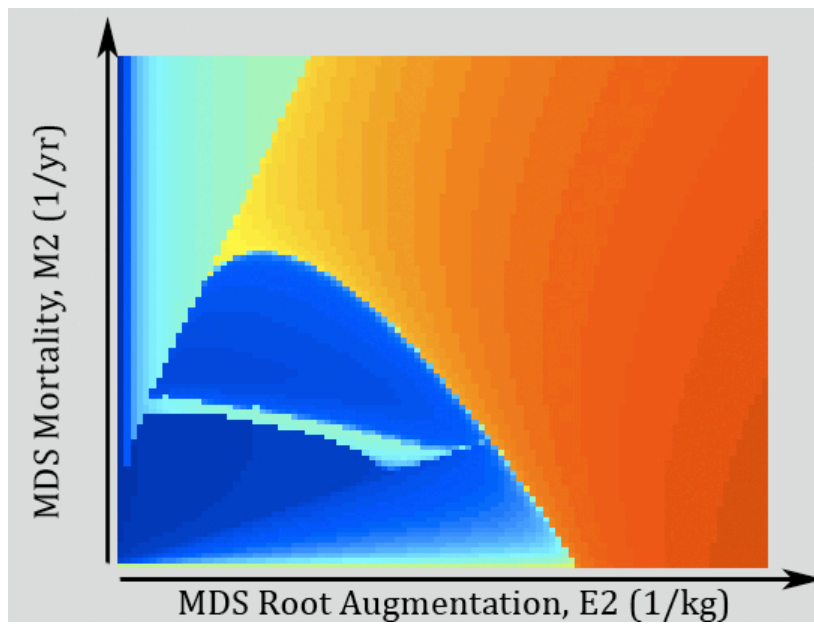


Figure 8 Productivity of the ecosystem. Like figure 6 this figure shows the sums of the average biomass values of the (LMS,MDS) equilibrium state but now for the parameters precipitation and mortality of MDS (represented by figure 7d). Coexistence shows the highest productivity. Oscillations do not show raised productivity.

Hysteresis can be inferred from the demonstrated multi-stability. For testing hysteresis precipitation can be the bifurcation parameter. Then the four plots can represent the initial conditions in which the system is found. So if the theoretical simulation starts in the dark blue realm representing the (0,0) state then plot a) must be inspected because it considers (0,0) to be the initial condition. If the precipitation is increased (Arrow 1) and the plot goes to the turquoise realm that represents the (LMS,0) state then plot b) should be inspected as it has initial conditions (LMS,0). Further increase in precipitation (Arrow 2) leads to a yellow realm that is the (LMS,MDS) state then figure d) must be inspected as it considers initial conditions to be (LMS,MDS). Decreasing precipitation (Arrow 3) leads to a shift into the oscillatory realm followed by the (LMS, 0) realm so figure b) is considered again. A further decrease in precipitation leads to the (0,0) realm so figure a) should be considered again to complete the cycle. When there is a difference in precipitation value where the transition from one state to the other and back takes place this can be considered to be hysteresis.

Using this method to show hysteresis it can be derived that for the oscillating state (red) it is not possible to obtain oscillations through the (LMS,0) equilibrium state, because there is no red band in figure 7b. Therefore oscillations can only be achieved through a decrease in precipitation in the (0,MDS) and (LMS,MDS) equilibrium states.

With increasing precipitation the productivity also increases (Fig. 8). The bands of oscillations, like in figure 6, give rise to bands of heightened productivity. Coexistence, which occurs at higher precipitation values, leads to the highest productivity levels.

Results - Fieldwork

Successional Order

When comparing the correlation between the canopy and the mound radii of the two species there is a difference in the correlation coefficient (Fig. 9). Both correlations are highly significant. For *A. serratuloides* the Pearson's correlation coefficient was 0.808 with significance at the 0.01 level. For *N. mucronata* the Pearson's correlation coefficient was 0.501 also with significance at the 0.01 level. The difference in the coefficient shows a higher correlation for *A. serratuloides*. Successional order can be indicated from the correlation. In Fig 9 we see that most of the mound size is caused by *A. serratuloides*.

Root Augmentation

The ratio between the above ground biomass and the lateral root length represents the parameter value E in the model. This relationship is very difficult to visualize clearly (Fig. 10). What can be derived from the figure is that *N. mucronata* has a larger lateral root length per unit of above ground biomass than *A. serratuloides* though the difference is far less than expected. Statistical analysis shows that the Pearson's correlation coefficient for *A. serratuloides* is 0.576 with significance at the 0.05 level whereas the Pearson's correlation coefficient is 0.317 without significance for *N. mucronata*. This shows there is a difference in coefficients but only one of them is significant enough to draw conclusions.

Grazing

There is a difference between the two species in the effect of grazing on the relation between the canopy and mound radii. For both species the canopy radius decreases compared to the mound radius in grazed areas (Fig. 11). The difference is not the type but the magnitude of the relationship. The figure demonstrates that the effect of grazing is higher for *N. mucronata* than for *A. serratuloides*. Statistical analysis shows that the Pearson's correlation coefficients for *A. serratuloides* differ less between the grazed and ungrazed conditions than for *N. mucronata*. The Pearson's correlation coefficients for *A. serratuloides* for the grazed condition is 0.638 and for the ungrazed condition is 5.37 (both with significance at the 0.05 level). The Pearson's correlation coefficients for *N. mucronata* for the grazed condition is 0.618 and for the ungrazed condition is 5.25 (also both with significance at the 0.05 level).

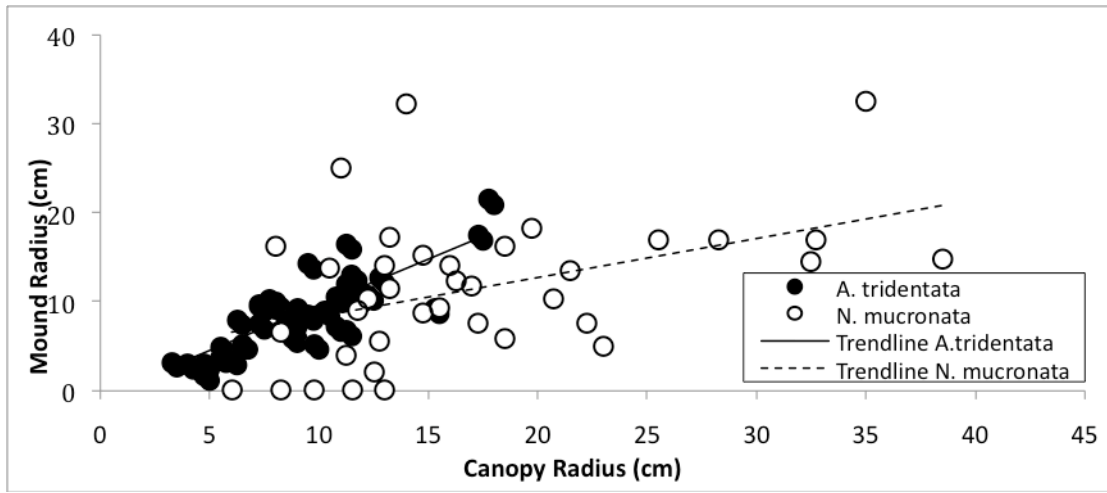


Figure 9 Successional Order. The difference of correlation between mound radius and canopy radius between *A. serratulooides* and *N. mucronata* implying successional order and infiltration effect.

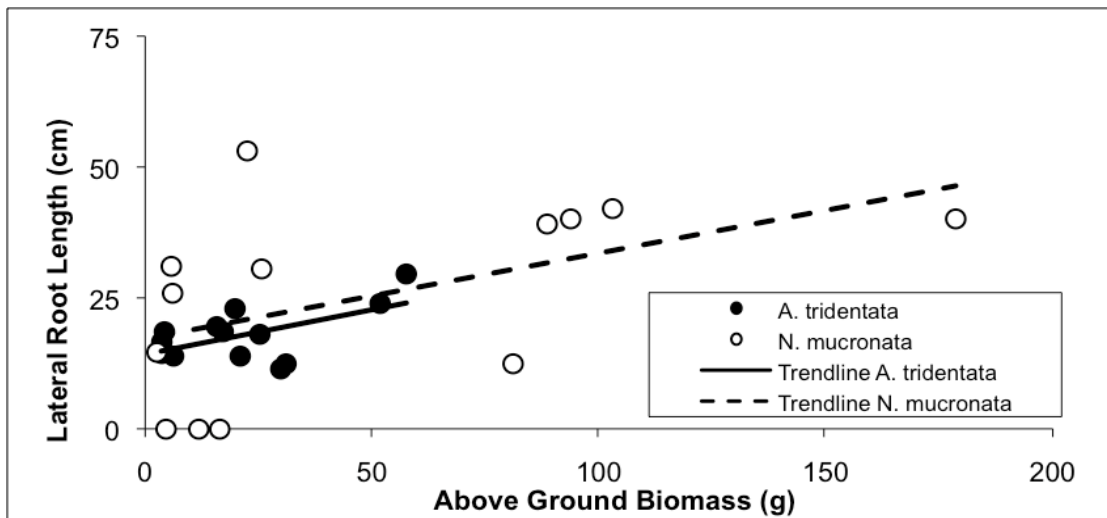


Figure 10 Root augmentation. The relation between above ground biomass and lateral root length for the two species, implying a difference in values for the parameter value E.

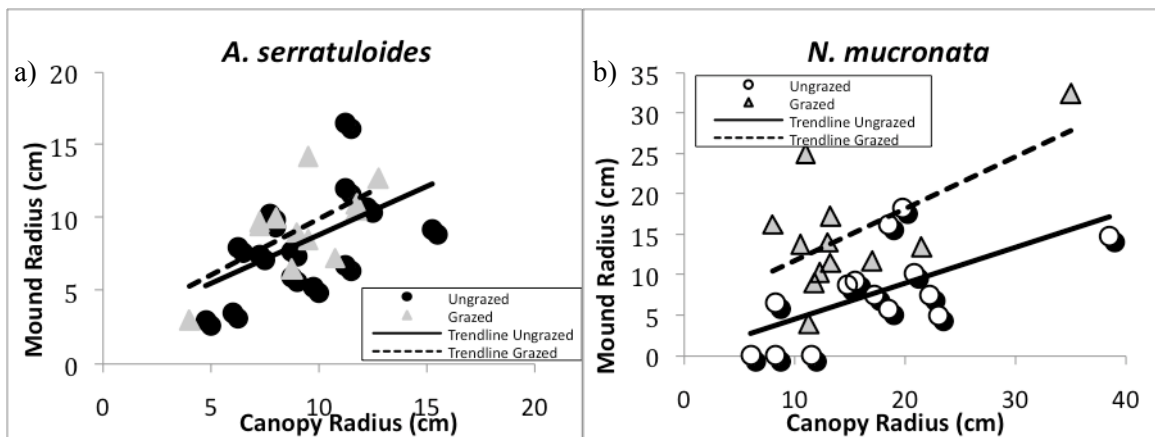


Figure 11 Grazing. a) Effect of grazing on correlation between canopy and mound radius for *A. serratulooides*. b) Effect of grazing on correlation between canopy and mound radius for *N. mucronata*.

Conclusion & Discussion

Conclusions

The parameters that determine a species character and allow for the representation of the LMS and MDS are Ψ , for infiltration feedback and E , for the root augmentation feedback. M , the mortality rate and P , the precipitation rate, are environmental factors that can aid in obtaining conditions for oscillations. The different outcomes of the model are, as predicted in H1 (see page 8), the four equilibrium states (one zero, two pure and one mixed state) and two oscillation states (one pure and one mixed). The zero state appears in two conditions. The first is where precipitation is too low to sustain the system. The second is where the competition between the two species is so fierce that neither survives, leading to cross annihilation. This latter result is found within the MDS dominance realm as a prequel to the oscillations. Multi-stability and hysteresis are shown in figure 7. Though the exact manner in which oscillation influence hysteresis is not demonstrated, as is predicted in H2.

From the fieldwork the following could be concluded. There is a stronger correlation between size of the canopy of *A. serratuloides* and the size of the mound than between the size of the canopy of *N. mucronata* and the size of the mound, as predicted in H3. This difference in the correlation suggests that *A. serratuloides* causes the formation of the mound and that (assuming the mound has a positive effect on the infiltration) *A. serratuloides* would have a larger influence on infiltration, making it the LMS. The reason why *N. mucronata* also had a significantly correlation can be explained by considering the influence of increased water availability by the mound. This leads to increased tolerated biomass levels, as was predicted in H4. The lack in significance for the root augmentation of *N. mucronata* makes it difficult to conclude that *N. mucronata* had a larger root augmentation, which was predicted in H5. Without this certainty we cannot conclude that it properly represents the MDS in our model. The grazing comparison shows that *N. mucronata* is more effected by grazing and should have a larger M coefficient, as is predicted in H6.

Overall the field example does provide a good example of the two species model, except for two points, as is predicted in H7. The first is that the mound remains after being constructed by the LMS. This results in a prolonged infiltration effect that is not incorporated in the model. The second point is that the root augmentation results were insignificant. Without concluding that *N. mucronata* represents a proper MDS the two species system cannot be properly represented.

Model Discussion

Figure 2 shows that the range of parameter values at which oscillations may occur are heavily dependent on the initial conditions. Figure 2c shows that oscillations may occur for parameter

values of $E2 = 2.3$ and $M2 = 2.2$. Comparing the values of $E1 (= 3.5)$ to the minimal $E2$ value for oscillations ($= 2.3$) gives a striking result, $E1 > E2$. Oscillations can occur for a less competitive MDS, but only for MDS dominant initial conditions. For dominant LMS initial conditions (figure 1b) no oscillations occur. The MDS is prevented from growing at all. This inhibition by the LMS does not properly represent the BCH and the MDS conditions do not properly represent a MDS. This could imply that the outcomes are too dependent on the initial conditions. It can be argued that the introduction of perturbation would relieve the MDS from the inhibition and that a pure LMS stable state would be impossible. However such perturbations should not be represented through the mortality term but should rather be a single or cyclic event.

For the zero (figure 2a) and co-dominance (figure 2d) initial conditions the true interactions are shown. For high $M2$ and low $E2$ the LMS is dominant, because the MDS parameter values make it non competitive. For high $E2$ the MDS is very competitive and outcompetes the LMS when given the opportunity. In between these two dominance realms is an area of coexistence. Coexistence is made possible because the relation between two parameters that determine the competitiveness of the MDS ($E2$ & $M2$) make the MDS as competitive as the LMS. This concept coincides with Neutral Theory, introduced by Hubbell (2005) to explain why diversity exists within the same niche. Tilman (2004) used this theory in combination with niche tradeoffs to propose that a slight decrease in resource level would result in a large decrease in probability that the corresponding propagule would survive. It also coincides with his R^* idea (1990). The spread of the coexistence realm is purely determined by the initial condition. This realm is always, per definition, in between where the MDS starts becoming competitive (the boundary between LMS dominance state and any other state) and where the infiltration effect of the LMS is present (boundary between MDS dominance realm and any other).

The three bands found within the MDS dominance realm show a specific effect of the interactions between the two species and their mechanisms. First of all to find an area of such radical interactions within the MDS dominance realm is unexpected. If such behavior is expected it should be in the boundaries between the two species, where generally coexistence is the stable state. In this area the maximum exposure between the two species is found. Secondly the three types of behavior are difficult to explain but can be understood when following the line of increasing MDS mortality. With the lowest MDS mortality the MDS outcompetes the LMS, simply due to its more competitive tradeoff balance. When increasing the MDS mortality it becomes less competitive until an area is reached where both species go extinct, termed cross annihilation. In this area, as it is within the MDS dominance realm, the MDS should be able to survive under these parameter values but it does not. This means the

LMS must cause the extinction. The main mechanism at work here is that both biomass levels are near to zero but the MDS is slightly higher causing suppression on the LMS and its infiltration effect. Without the infiltration effect the MDS will not grow and with the MDS larger than the LMS the LMS will not grow.

As the MDS mortality is increased this suppression is lifted because of the decrease in competitiveness of the MDS. This leads to the next band where the LMS is dominant. Figure 3 gives an example of the simulation, where it seems as though both species go extinct and suddenly the soil water peaks and the LMS follows. This behavior does not seem to have an ecological explanation. It is not an ODE solver issue as all solvers show the same outcome. It is intrinsic in the model meaning there must be an explanation why the MDS does not react to the peak in soil water. The explanation can be found when comparing the conditions just after the peak to the conditions found in the top right corner of figure 2b. This area under normal initial conditions shows a dominance of the MDS species though when the initial conditions favor the LMS the MDS never gets the opportunity to grow. There is a suppression of the LMS on the MDS because the LMS consumes all the water entering the system, never allowing the MDS to grow. This same suppression is working on the MDS in figure 2b, just after the spike.

As the MDS mortality is further increased the LMS dominance gives way to oscillations. This is because the MDS never gets the opportunity to suppress the LMS to the same extent as it had done in the two cases before. Figure 4 shows a long lapse time between the oscillations in which the MDS is suppressing the LMS but due to its higher mortality it eventually cannot maintain the numbers to maintain the suppression. This cyclic behavior was necessary to find parameter values that the MDS should have in order to properly represent a MDS.

It is questionable whether the cross annihilation state and spike condition are not simply a result of the definition that biomass values above 5% of the maximum (K) determines whether a species is present or not. This would imply that there are values for LMS and MDS under 5% but larger than zero. Of course this is the case but then the question becomes where between 0% and 5% of the carrying capacity is a species present? The definition was necessary in order to simplify the average biomass graphs (figure 5) into the various stable states from which meaningful conclusions could be derived. It is necessary to look at what happens to the biomass values when they approach to zero. These simulations have been run and show a general trend, representing the inhibition explained above. However, the proper question is the following: Is there no chance that the LMS would also spike under these conditions if the simulation time were to be extended towards infinity? It is unsure what

would happen, as there is no explanation as to why the LMS spikes at the arbitrary places it does. However from figure 3 you can see that the crude 5% definition is not relevant.

Figure 2c nearly shows an origin from which the different bands come together. From this origin onwards as the root augmentation is increased the bands are pulled apart and the bands become clear separate entities. The mortality range for oscillations also increases as the root augmentation is increased. This is the effect that the root augmentation has with respect to mortality on the parameter space location at which oscillations occur. Increasing mortality does not have such a clear response on the parameter location of the oscillations. It merely allows for going from one stable state to the other (vertical manipulation in the figure). From figure 7 the effect of precipitation with respect to mortality on the parameter location of oscillations can be derived. Here there is not such a clear effect as for root augmentation. However it can be seen that increasing mortality drastically decreases the precipitation range for which oscillations are found.

Lopez-Ruiz & Fournier-Prunaret (2009) published three papers that cover the competitive interactions between two species. One of these three papers discusses how the phenomena of coexistence, oscillations and chaos are present in the two species system and thus in nature through two coupled logistic equations (Lopez-Ruiz & Fournier-Prunaret 2009). Horn & Catron (2003) also considered oscillations and chaos in population dynamics. They looked at the plankton paradox developed by Huisman & Weissing (2001) that stated that even with the simplest models of competition that three species are sufficient to generate oscillations, and five species enough to generate chaos. From this they concluded that oscillations and chaos are fairly easily generated when individuals can influence one another. Nedorezov & Nazarov (2000) concluded from their model that in discrete models of competition, oscillations could be explained by dependence of population growth rate on population size at previous time. Sherratt *et al.* (2009) discusses that systems undergoing invasion, as would be the case for the LMS, often generate periodic spatiotemporal oscillations. These patterns then may give rise to chaos. Sherratt *et al.* (2008) show relevant field studies of cyclic populations that may also be represented by oscillatory behavior.

Figure 5 is very helpful in determining the influence of parameter changes on the biomass of the two species. Within the band structure it is clear that increasing MDS mortality results in gradually increasing LMS values, until oscillations take place. The oscillations are influenced by the increasing MDS mortality in the form that the LMS suddenly vanishes whereas the MDS values gently increase. The boundary is the location where the LMS goes extinct and the MDS resumes dominance and decreases in value as MDS mortality is further increased.

This figure allows for the clarification of how the oscillations might be influenced by precipitation and mortality changes.

Figures 6 and 8 show the productivity of the system, which is simply the sum of the average biomass values. From these figures it can be concluded that after the zero state the pure MDS state gives the least productivity. The pure LMS state is relatively more productive but coexistence is the most productive. In general, when the MDS outcompetes the LMS the productivity drops because the modulation effect is gone meaning there is no more increased infiltration. The productivity is the highest when both species are present. Wright & Jones (2004) found that with increasing productivity through ecosystem engineers there is a coupled increase in species richness, supporting the results.

The most important conclusion that can be drawn from figure 7 is that oscillations will only occur for decreasing precipitation or MDS mortality, from initial conditions where the MDS is present. This is because with increasing precipitation or MDS mortality the pure LMS state always precedes the oscillations. As the pure LMS initial conditions (figure 7b) never gives rise to oscillations they will never occur for increasing precipitation or MDS mortality. The arrow example given shows hysteresis with precipitation as the bifurcation parameter. However the direct influence of oscillations cannot be drawn from it. In order to find out the exact influence of oscillations on hysteresis, hysteresis plots should be made for different parameter values, resulting in a crossing of the boundary at different times in the oscillation cycles. As the oscillations possibly represent all four equilibrium states in one, the influence on hysteresis is dependent on exactly where in the cycle the boundary is crossed. This implies chaotic behavior because the possible results are dependent on the exact initial conditions. This emphasizes the earlier mentioned notion that the model is too dependent on its initial conditions. The effect on hysteresis is important to understand because of its implications concerning catastrophic shifts (Rietkerk *et al.* 2004).

Model Criticism

The P range for which oscillations occur is around $40 < P < 600$. This range does not properly represent precipitation as the P value only becomes a precipitation rate when multiplied by I (which is A for fully vegetated conditions). For $A=40$, this gives a range of $1600 < P \cdot I < 24000$ (kg yr^{-1}). In order to represent a desert the precipitation should be less than 250 mm yr^{-1} . Even though the units are different this is a large discrepancy. The P range could be changed without drastically influencing the results by changing parameter values that have been kept similar to those used by Gilad *et al.* (2007). This would change the characteristics of the plants or environment considered. The parameters are now set to represent shrubs in arid environments. It would be interesting to investigate the possibility of changing the parameters

so that the oscillations occur at realistic precipitation values. From figure 7 it is clear that at P values of 20 (= 800 kg yr⁻¹) there is no biomass growth, which is expected for such a large amount of water. This indicates the absolute values for precipitation are incorrect but the relative results are correct. This mistake can be explained by considering the equations of Gilad *et al.* who also use a surface water term, expressed in mm. This term was responsible for the infiltration term, meaning that a conversion factor (from mm to kg) might be missing somewhere.

The fact that productivity is highest for coexistence (figures 6 & 8) could be a direct effect of the modeling approach taken. By simply adding another species to the system the total maximum allowed biomass in the system is double, $K_{LMS} + K_{MDS}$ instead of just one K value. Even though the total maximum biomass in the system is doubled this should have no influence on the relative amounts of biomass between the two species, so the relative results are still valid. The argument defending the model is that even by adding additional species the water still limits the system and so there should be no increase in the productivity. The model shows results for very high P values meaning the system limitation by water is probably reduced.

The addition of growth potential as a result of increasing the total K by adding species has another drastic effect. The evaporation term taken from Gilad *et al.* (2007) on which my formulas are based states:

$$Evaporation = -N(1 - \sum_{i=1}^n \frac{R_i B_i}{K_i})W$$

Where n represents the number of species and i the number of the species in consideration. When expanding the formula to two species and assuming the same R for every species the result is the formula used in this model:

$$Evaporation = -N(1 - R(\frac{B_1}{K_1} + \frac{B_2}{K_2}))W$$

The problem arises when assuming full vegetation ($B_1=K_1$ & $B_2=K_2$). This results in:

$$Evaporation = -N(1 - R(1 + 1))W$$

Now the reduction of evaporation due to shading is larger than evaporation itself (as another species with additional biomass produces more shading). The evaporation term becomes positive instead of being a negative (loss) term. This results in plant water uptake being the only way for the system to lose its water and the lack of a loss term drastically influences the

stability conditions of all the states. When the water content of the model is large, which is the case with high P values, the effects are even more drastic. This could have serious implications for all the results. To eliminate this issue I suggest changing the general formula into the following:

$$Evaporation = -N(n - \sum_{i=1}^n \frac{R_i B_i}{K_i})W$$

Replacing the 1 by the term n makes it a variable that allows for the consideration of n number of species. This way the evaporation reduction can never be greater than the evaporation itself, keeping the evaporation term negative. Now this term is properly represents a loss term and there will always be a possibility other than the uptake term for the system to loose its water.

I repeat that in theory as long as the water availability is the limiting factor that the original term for evaporation should have no drastic influence. However when K becomes the limiting factor this quickly changes. For certainty it would be beneficial to change the evaporation term to the suggested term.

In order to render the results useful again simulations were run for an extremely simplified version of the model. The details can be found in appendix 2. This simplified, one species model also showed oscillations. This implies that the precipitation values at which the oscillations occur are arbitrary and they are dependent on the specific values chosen for all the parameter values. It also shows that the original evaporation term is not responsible for the oscillative nature of the model, but rather that it is intrinsic in the model. The only factor kept constant was the water uptake and plant growth term, which are both dependent on the same factor $(1+EB^2)$. Therefore this term is probably responsible for the oscillations.

Future Modeling

For future research it would be interesting to introduce more than two species, each with an increasing investment in roots compared to the last. Under these conditions it would be possible to see a wave propagating from one species to the next, to show the BCH more articulated. Beninca *et al.* (2009) showed in complex plankton foodwebs that coupling of predator-prey oscillations could lead to chaotic behavior. It would also be nice to have the model go into spatial dimensions to see not only temporal, but also spatial waves and patterns. In addition it would also be beneficial to introduce dispersal strategies to the model. Pueyo *et al.* (2008) have investigated these in relation to vegetation patterns in arid environments. Boeken & Orenstein (2001) indicated how mounds and litter might influence seed dispersal. Smith *et al.* (2008) investigated the effects of density-dependent dispersal on

the spatiotemporal dynamics of cyclic populations. Their conclusions can be of great use for implementing dispersal into the model.

Introducing periodicity through precipitation cycles and perturbations would also be a possibility to obtain oscillatory patterns. This would resemble a method used by Qian *et al.* (2010), who used impulsive control to study the dynamic behavior of predator-prey systems. However using this method would not utilize the oscillatory behavior of the predator-prey system, but rather result in a systematic synchronization of the system to the oscillating initial conditions representing the abiotic environment. These perturbations would allow the pure states that are very stable to be disrupted, creating a different cyclic character.

In order to properly study what causes the oscillations and by what changes they are influenced more research is necessary. This would be interesting because the oscillations may be able to function as natural signals indicating either a strengthening or weakening of an ecosystem. Figures 12, 13 & 14 are shown in appendix 1. These figures give an example of how to check the influence of precipitation, mortality and root augmentation on the frequency of oscillation. They show that precipitation does not influence the frequency of oscillation but root augmentation and mortality do. In general when the MDS becomes more competitive the frequency decreases. The implications of such information could be greatly aid our understanding of ecosystem functioning.

Fieldwork Discussion

The conclusions drawn for the fieldwork support the idea that *A. serratuloides* is responsible for the initial build up of the soil mound. Therefore it is safe to assume a higher influence on infiltration and thus a good representation of the LMS. However *N. mucronata* can also be found on mounds, meaning it too can profit from the increased infiltration when *A. serratuloides* is not present. This implies that after the mound is constructed it remains present after *A. serratuloides* has died. This means that the infiltration effect remains after the departure of the ecosystem engineer. Though in our case the MDS consumes all the water added by the modulation effect. Hastings *et al.* (2007) investigated the temporal and spatial roles of engineers and found that often the engineering effect outlives the engineer. From this they suggested ecosystem engineers might facilitate restoration. Byers *et al.* (2006) suggested a conceptual framework that shows how ecosystem engineers can be used to assess the likelihood of restoration of a system to a desired state. This effect has not been taken into account in the model and could have serious consequences for the survival of the MDS during oscillations.

Furthermore the inability to draw conclusions about the root augmentation results of *N. mucronata* makes it difficult to compare it to a MDS. This adds to the inaccuracy of the

comparison between the field example and the model. Taking more samples for *N. mucronata* may increase the significance of the correlation and could eliminate this problem.

Finally the differences in the effects of grazing on the size of their canopy compared to the size of the mound is a good way to express the effect of grazing on mortality. To assume grazing could represent the whole mortality term is a weak assumption. Investigating the other processes that influence the mortality term could increase the power of this assumption. However when working with the model it was possible to obtain oscillations without having a discrepancy in the mortality term. If the mortality terms were assumed to be equal the other parameter values would have become unrealistically high.

Fieldwork Criticism

The interactions between *A. serratulooides* and *N. mucronata*, based on the fieldwork done, do not perfectly represent the two species of the mathematical model. The fieldwork is not convincing enough to convey a cyclic character. There are interesting mechanisms in the form of feedbacks that indicate cyclicity but this cannot be concluded on the basis of the measurements taken. Therefore a complete idea of BC is not represented. However the example may represent a small-scale succession cycle between a nurse-plant and its protégée that most probably is a nurse-plant for another protégée. This succession cycle is only cyclic when assuming that there is a transition to a bare crust state. Then cyclicity would follow from knowing whether the pioneer really prefers bare land or not. What the measurements do show is a definite morphological difference between the two species that occupy the same area. The difference can be related to the function these species might have, though this would require more intensive research. Yeaton (1978) demonstrated an established succession cycle where the presence of *Larrea tridentate* and *Opuntia leptocaulis* alternate in a cyclic manner. In order to conclude that the two species I consider are part of a succession cycle like the one by Yeaton more thorough research is necessary. Even if this is established there is a difference between BC and succession cycles. BC explicitly considers many species, often of the same genus or family that fill the same niche, which is slowly changed over time. Cyclic succession is simply an extension of the idea of succession.

The fieldwork was done at the beginning of the dry period. In theory this would be a good time to conduct fieldwork as the plants consumed most of the water from the rainy winter period. However the research results were after a succession of relatively dry winters meaning the surviving individuals were severely strained. When digging for the root systems it often occurred that a specimen had no roots and had become deceased. This partially explains why there is such high variability in the results and a lack of significance in some cases.

Future Fieldwork

For future research it would be interesting to take more samples of both species. Then the samples could be split into three categories per species; small, medium and large. When correlating the canopy to the mound sizes *A. serratuloides* would correlate for all categories, whereas *N. mucronata* would only correlate for the large, and maybe medium, categories. This would properly show that as *A. serratuloides* grows it enables the mound to grow.

General Discussion

It can be questioned how far the relation between competition and predation can represent the results found. Competition is viewed as the first interaction that limits diversity, whereas predation only changes the effects of competition. Chesson & Kuang (2008) suggest that this is not realistic and that the two interactions should be viewed symmetrically. They state, “The two interactions are equally able to either limit or promote diversity”. This equality could also explain the oscillations found in this research that only contains competition as a negative interaction between the two species. Kuang & Chesson (2008) look at the effects of predation and competition on coexistence. They found that when competition is not strong enough to cause endogenous population fluctuations, predation could induce fluctuation-dependent coexistence by destabilizing the equilibrium (Kuang & Chesson 2008).

In general it is important to question in how far the found oscillations represent an example of the BCH. The oscillations clearly show a very interesting phenomenon in the two species system considered but the assumption that they represent such a broad theory is debatable. The main argument is the relation between the selected feedback mechanisms and the functional species groups of the BCH. Next to this the fieldwork results indicate a short succession cycle. Again it is important to question in how far this cycle represents an example of the BCH. To answer these questions it is important to note that this research is only a limited example of the BCH. The model and fieldwork do not try to show or predict the full implications of the BCH. They rather try to investigate the basic mechanisms by which cycles in nature can be explained.

This investigation can add to insights as to how succession can be influenced by the presence of different types of species. The presence of an ecosystem engineer will often imply the presence of a species that is dependent on the engineer, and if not there is a niche waiting to be filled. The conclusions drawn shed light into how such species may interact and what the influence of these interactions can be on ecosystem stability in the form of hysteresis. Succession cycles and Biodiversity Cycling are ideas that can aid the understanding as to how ecosystems are built from barren or disturbed land. The role of ecosystem engineers is clearly to upgrade (or downgrade) the quality, productivity or even efficiency of the ecosystem, when

putting it into the BCH context. These are interesting theories when investigating possible anthropogenic ways to aid nature in restoring habitats. It is not the exact values at which the interesting mechanisms are shown that are interesting to know, but the understanding and general conclusions drawn from those mechanisms.

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Appendix 1 - Effect of precipitation, MDS root augmentation and MDS mortality on the frequency of the oscillations

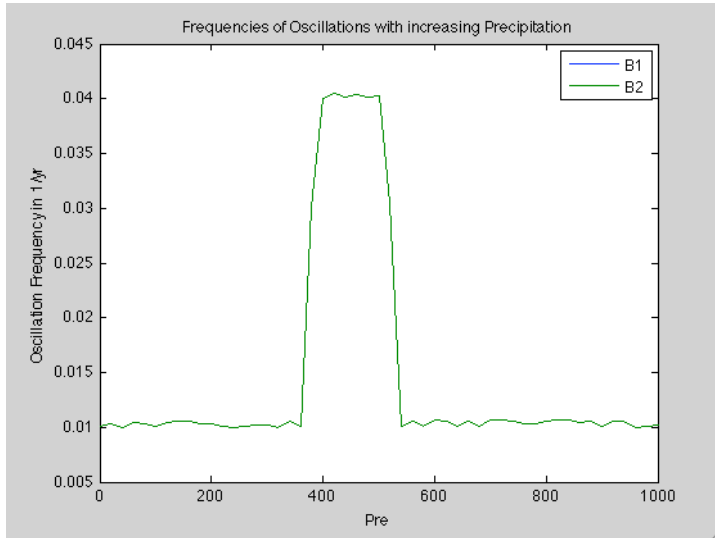


Figure 12 Effect of precipitation on oscillation frequency. Oscillations occur for the range $380 < P < 580$. The frequency jumps up from the baseline (0.01 yr^{-1}) to a frequency of 0.04 yr^{-1} . This means one cycle is complete every 25 years. A slight change in P has no influence on the frequency, except for that it either oscillated or it does not.

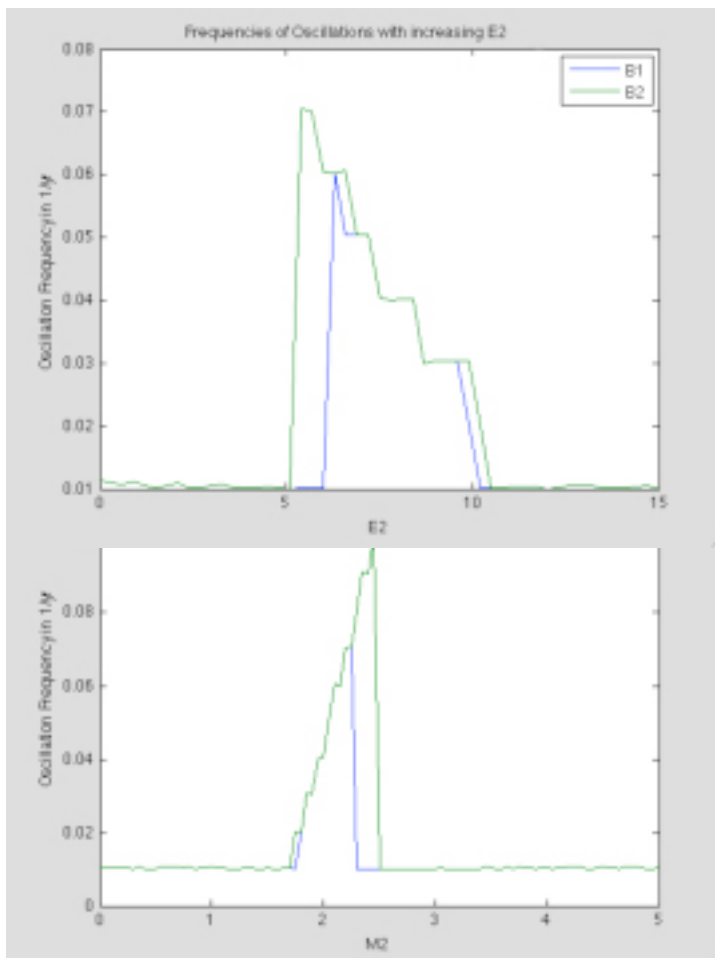


Figure 13 Effect of MDS root augmentation on oscillation frequency. Oscillations occur for the range $5 < E2 < 11$. The frequency jumps up from the baseline (0.01 yr^{-1}) to a frequency of 0.07 yr^{-1} . As E2 is increased the frequency slowly decreases, meaning that as MDS becomes more competitive the frequency decreases.

Figure 14 Effect of MDS mortality on oscillation frequency. Oscillations occur for the range $1.7 < M2 < 2.5$. The frequency slowly increases from the baseline (0.01 yr^{-1}) to a frequency of 0.1 yr^{-1} . As E2 is increased the frequency slowly increases, meaning that as MDS becomes less competitive the frequency increases.

Appendix 2 – Simplified one species model that shows oscillations

For the simplified model only the MDS species was considered. The evaporation term was linearized. The growth and uptake terms were kept constant but the parameters responsible for their strength were set to 1. The following results are the results:

$$\frac{dW}{dt} = P - NW - (1 + EB)^2 BW$$

$$\frac{dB}{dt} = (1 + EB)^2 WB(1 - B/K) - MB$$

The Jacobean matrix of these formulas gave Eigen values with complex parts implying that the for certain P values there were oscillations. This becomes clear in figure 15.

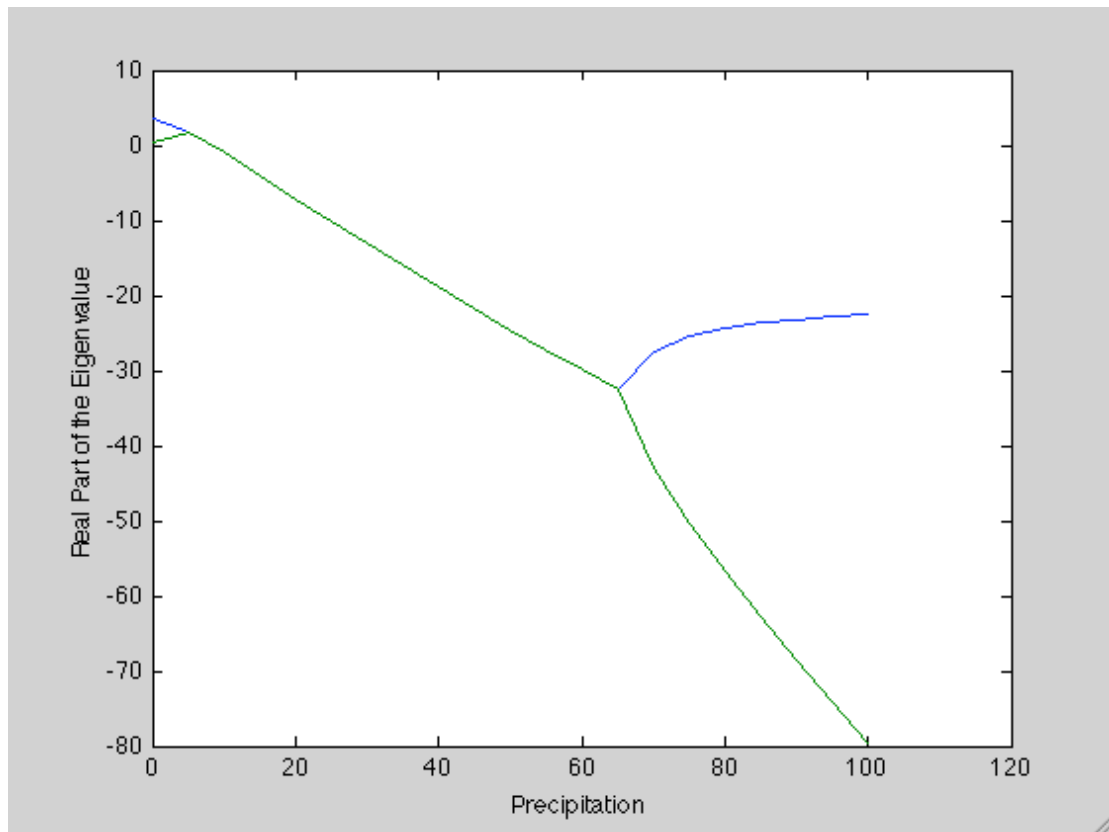


Figure 15 Finding oscillations for varying precipitation values in a simplified model. Where the two lines come together there exists a imaginary part of the Eigen value of the Jacobean matrix of the model. Where there are imaginary numbers as a result of the Jacobean there is oscillatory instability. Oscillations occur for the range $4 < P < 66$. This graph implies that oscillation occur for the simplified model in which there is a linear evaporation term and completely different precipitation values. This implies that these two factors are not responsible for the oscillations but rather that a factor that is still in the model is responsible.

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